ISLAND ECOSYSTEM STABILITY AND METROSIDEROS DIEBACK*

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INTRODUCTION

Elucidating the concept of island ecosystem stability was the unifying theme for our ecological and evolutionary research approaches of the Hawaii contribution to the US/IBP (International Biological Program). Several well-known 19th century naturalists including Darwin (1859), Wallace (1880) and Hooker (1867) had gone on record saying that oceanic island biota are relatively fragile because they evolved in isolated environments. Island biota are thus not equipped to compete successfully with continental biota once these become dispersed to islands by human activity. This general hypothesis was repeated in this century by many authors, including Degener (1930), Carlquist (1965) and others, and it was more-or-less adopted as a truism.

It was therefore not surprising that when the Metrosideros rain forest decline or dieback problem surfaced in the seventies with its spatial magnitude across the east-flanks of Mauna Kea and Mauna Loa (Burgan and Nelson 1972, Petteys et al. 1975) that the US Forest Service and Hawaii State Department of Land and Natural Resources thought a new epidemic had entered this native ecosystem. It was like a verification of this long-standing prediction of doom.

Now that we know a great deal more about the Metrosideros dieback phenomenon; first of all that it is not caused by a foreign disease and then not even by an indigenous biotic agent (Papp et al. 1979) but rather by the population behavior of Metrosideros itself interacting with certain site factors (Mueller-Dombois 1982 a,b,c), the question still remains: Is this large-scale dieback phenomenon not an expression of

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biological instability? If it is, then the Hawaii IBP answer as given in the 1981 synthesis volume (Mueller-Dombois et al. 1981) may need revision.

I will therefore first briefly review the island ecosystem stability concept as understood through our IBP research and then relate this answer to the new findings about the Metrosideros dieback phenomenon.

HAWAII IBP STABILITY HYPOTHESES

Ecosystem stability is a complex concept involving many biological and environmental interactions. It relates to populations, species and communities and their dynamic responses, to internal as well as external perturbations of all kinds. It does not mean simply constancy in time as does the ecological concept of climax. Instead, ecosystem stability refers to its resistance to stress or persistence under stress and the ability of the system to return to equilibrium (Preston 1969).

In the Hawaii IBP we reduced the concept to mean community resistance to exotic species invasion and the survival capacity and adaptability of indigenous biota. We further partitioned the stability concept into a number of testable working hypotheses that we thought may serve as stability indexes. These were: first that community stability is positively related to species diversity; second that stability is positively related to life-form diversity; third that stability is related to climatic factors; and fourth that stability is related to the behavior of the dominant community-structure forming life forms.

Only the fourth of these possible indexes of island ecosystem stability proved worth further scrutiny. The others turned out to be unreliable. These relationships are discussed in detail in the final two chapters of the Hawaii IBP Synthesis Volume (Mueller-Dombois et al. 1981). These tests brought out, further, that many indigenous island community members consist of ecologically surprisingly versatile species. For example most of the island tree species are adapted to a wide ecological spectrum. They can grow on rocks, logs and mineral soil. Many can grow on wet and dry substrates and on nutritionally rich and poor, even toxic soils. Nearly all native trees investigated can reproduce vegetatively as well as from seed. Most of the indigenous rain forest epiphytes can also grow on the forest floor if not disturbed

by pigs. The majority of island species were found to be peculiar generalists, not extreme specialists as had been thought before.

The microevolutionary focus was on the genetic properties of island species. It was found that island populations contain as much genetic variability as continental populations, and further that island populations track environmental changes genetically just as vigorously as do continental populations. Therefore, island populations -- except for a few exceptionally specialistic ones -- are not at an evolutionary dead end as has often been assumed (Carlquist 1980). These new findings are summarized in H. L. Carson's synthesis chapter 14 (in Mueller-Dombois et al. 1981).

Our focus during IBP was to concentrate on a few selected, relatively undisturbed indigenous communities and ecosystems. We thought that after we have gained some base-line information on how indigenous communities and ecosystems are put together that we then can understand better how they may function under stress. Therefore, the 'ōhi'a (Metrosideros polymorpha) dieback problem did not receive much attention under IBP. It is therefore of some interest to now re-examine one of the main IBP conclusions with regard to the dieback. This conclusion was that island ecosystems are just as stable as continental ecosystems provided that we adopt an enlightened policy for conservation management.

METROSIDEROS DIEBACK ETIOLOGY

Large-area canopy collapse has occurred in the Hawaiian rain forest recently (Petteys et al. 1975) and in the past (Lyon 1909, 1919). In both cases the canopy collapse was not caused by disease or any new human-induced stress. Canopy tree dieback thus is a dynamic property inherent in the Metrosideros rain forest itself. Moreover, it is interesting that such dieback is not restricted to the Hawaiian Islands, but occurs also in the Metrosideros forests of New Zealand (Stewart and Veblen 1981, Mueller-Dombois 1982b).

In searching for the causes of the Metrosideros dieback in Hawaii we have come a long way from the disease and insect damage hypotheses to the natural stress and succession hypotheses. Since the dieback is often related to particular lava flow outlines and other distinct site boundaries, there is also a clear habitat relationship. This we recognized early (Mueller-Dombois et al. 1977) by giving names to three site-related dieback patterns, the wetland, dryland and bog-formation diebacks. Thus the idea of

climatic change as suggested earlier by Selling (1948) cannot be accepted as an explanation. However, climatic perturbations becoming effective through locality-specific factors are still a possibility. We are exploring this further through Bill Evenson's climatic perturbation analysis (presented in another paper in this symposium).

By considering all presently known facts and by surveying dieback stands in several other island communities inside (Mueller-Dombois 1981a, 1982c) and outside the Hawaiian Islands (Mueller-Dombois 1982 a,b), the etiology of the dieback leads to the inescapable conclusion that it is the ultimate manifestation of cohort senescing. Cohorts are members of the same regeneration wave that became established synchronously in an area following a perturbation. Perturbations that can set the stage for large-scale cohort invasion are for example lava flows, ash-blanquet deposits, landslides, flash floods, fire, violent storms and elimination of ice through glacial retreat (as on the South Island in New Zealand, Mueller-Dombois 1982a). Of course there must be species in such an area that are the wave colonizers following such catastrophic disturbances. We know that the Hawaiian Metrosideros polymorpha is such a species (Forbes 1912, Robyns and Lamb 1939, Atkinson 1970, Smathers and Mueller-Dombois 1974). It often invades new volcanic substrates in large cohorts. After these become successfully established, they grow to maturity synchronously and then into the senescing stage, also synchronously. Dying can result in further synchrony by high genetic uniformity of the cohort and possibly by transfer of nutrients from senescing leaves to reproductive organs, for example, during a strong season of flowering and subsequent seed development. Environmental factors contributing to further synchrony in death may, for example, be a gale or Kona storm that tears off a sizable leaf mass which then is not replaced due to senescence. Other environmental perturbations, such as temporary flooding of the feeder roots or a temporary soil drought may also contribute to synchronized death in different sites. Metrosideros cohorts of the same genetic stock growing on 'a'ā lava may grow taller and live longer than those growing on pāhoehoe flows. A pāhoehoe substrate may force a cohort into an early senescence due to low nutrient availability and nutrient imbalance.

During cohort senescing, the canopy opens and the light conditions on the forest floor become favorable for upward growth of new even-statured saplings to develop into the next canopy cohort. Uniform tree reproduction is what in fact happens in the more radical diebacks and the 'ōhi'a borer (Plagithmysus bilineatus) or the root fungus Phytophthora cinnamomi in certain

habitats may play a locally important role, as hasteners of the dieback and indirect helpers in the reproduction process. A new Metrosideros cohort becomes established and a second cycle begins. Generation turnover may occur several times in this manner, but each time the conditions change with regard to soil, seedbeds and undergrowth. The first canopy collapse is already a much lesser perturbation than the new lava flow or ash deposit that gave rise to the first generation.

So far we have distinguished five kinds of tree-group dieback (i.e., dryland, wetland, bog-formation, gap-formation and 'ōhi'a displacement, Mueller-Dombois 1981b). In terms of strictly spatial patterns, we have recognized (from aerial surveys) tree-to-tree and salt-and-pepper diebacks. Both can cover large or small areas. We have sometimes called the small-area tree-to-tree dieback "hot-spot" dieback (Jacobi 1982). The small-area salt-and-pepper dieback relates to the newly described (Mueller-Dombois 1981b) gap-formation dieback, which is also more typical for the Metrosideros dieback on Oahu (Gerrish and Mueller-Dombois 1980). Spatial dieback patterns may sometimes be sharply delimited by lava flows or other distinct site boundaries such as moderately well-drained ash deposits adjoining bogs.

From the viewpoint of dieback recovery we can distinguish two main patterns, namely 'ōhi'a displacement dieback (as occurring in the Ola'a tract of Hawaii Volcanoes National Park) and 'ōhi'a replacement dieback as occurring almost everywhwere else. However, replacement dieback may differ greatly in the quantity and dispersal of young 'ōhi'a growth and also in its quality. The most obvious quality differences relate to whether the 'ōhi'a reproduction is primarily from seedlings or vegetative from branch-layering. The latter is most common in the bog-formation dieback.

Yet, another more subtle qualitative difference seems to operate also. This is a genetic shift in the sense that the new cohort of seedlings may be genetically different from the dying canopy cohort. In other words, we hypothesize that the dieback cycles involve a successive turnover of 'ōhi'a races or ecotypes from pioneer to seral to near-climax 'ōhi'a.

In addition to spatial pattern and dieback-recovery variations we are also beginning to recognize temporal pattern variations such as fast versus slow diebacks and diebacks synchronized over large areas and those synchronized over smaller areas or in patches but out of phase with one another (Mueller-Dombois 1981b).

This brings me to the main question raised in this paper.

IS THE DIEBACK NEW EVIDENCE FOR ISLAND ECOSYSTEM FRAGILITY?

Cohort dieback of the dominant tree species clearly is a weak stage in the successional development of the Hawaiian rain forest. The areas with dead standing trees are a manifestation of the fact that there is no other tall tree species in the Hawaiian rain forest that has evolved to replace 'ōhi'a along a successional gradient. Instead 'ōhi'a itself evolved into its own successional replacer, and this replacement is not a smooth or continuous event but a periodically interrupted or oscillating process. Moreover, in the bog-formation dieback it is also a poor tree replacement process. This made Lyon (1909, 1918) think that the watershed values would become seriously impaired. He therefore suggested replacement by planting bog-adapted exotic tree species.

Unfortunately, what Lyon did not see was that a native vegetation cover had developed during and after the dieback, which reportedly was just as good in preserving the watershed values on East Maui as was the less boggy Metrosideros forest before. (Further details are given in Alan Holt's paper in this volume).

Therefore, the question of ecosystem stability must rest with the recovery process associated with dieback and its spatial dimension. If the recovery is such that soil erosion and nutrient loss is not accelerated, then there is no serious loss of ecosystem stability. Moreover, if exotic species invasion is not significantly encouraged during the dieback-recovery process, then also there is no loss of stability.

However, we have indications (Mueller-Dombois et al. 1977) that dieback invites exotic species invasion in areas where there are many exotic species in the neighborhood of dieback stands (as in Hawaii Volcanoes National Park), while dieback stands in more remote areas remain dominantly under native vegetation cover.

Our IBP research indicated that there is only one parameter that makes island ecosystems more fragile than continental ecosystems, and that is the generally smaller size of island populations and habitats. Therefore, large-area dieback areas are also more vulnerable than smaller dieback areas. In this connection it is interesting to note that the larger cohort sizes occur only on the Big Island. On Maui they are not as large and

on Oahu they are represented only by small groups of even-statured trees (Gerrish and Mueller-Dombois 1980). Thus rain forest development proceeds from larger to smaller 'ōhi'a cohort sizes along the primary successional gradient in the Hawaiian Islands, i.e. from geologically young to older. This also means that ecosystem stability remains essentially constant through the course of primary succession.

One important implication for conservation management which can be deducted from this long-term dynamic process is that ecological reserve sizes should be adapted to the spatial scale of dieback and recovery patterns in such a way that dynamically stable units are preserved in their entirety. Such stable units should include a complete set of forest life cycle stages. If this is not recognized, we will be faced inevitably with an instability dilemma insofar as we are preserving only a fragment of an ecosystem or self-maintaining watershed unit. This undoubtedly would lead to accelerated loss of native species and vegetation.

Finally, it should be said that there is no need at this time to modify the IBP conclusion that island ecosystems are inherently just as stable as continental ecosystems and that the only factor making island ecosystems more vulnerable to destruction are their generally more limited habitats and smaller population sizes.

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